What can South African reefs tell us about the future of high-latitude coral systems?

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ABSTRACT

Coral communities are found at high latitude on the East Coast subtropical reefs of South Africa. They are biodiverse, economically important, and afforded World Heritage Site status in the iSimangaliso Wetland Park where some are subjected to recreational use. While the Park's unique coral reefs have, to date, suffered little bleaching from climate change, they are susceptible to the phenomenon and provide a natural laboratory for the study of its effects at high latitude. This review covers recent advances in the regional oceanography; coral community dynamics and the underpinning reef processes, including minor bleaching events; the incidence of coral disease; and coral genetic connectivity. The effects of human activity (SCUBA diving, recreational fishing, pesticide use) were assessed, as well as the nursery benefits of *Acropora austera*, a coral which provides the reefs with much structure and is vulnerable to damage and climate change. The reefs were valued in terms of human use as well as services such as sediment generation and retention. The results have provided valuable information on relatively pristine, high-latitude reefs, their socio-economic benefits, and the anticipated effects of climate change.

1. Introduction

Coral communities in South Africa constitute the southernmost distribution of this fauna on the African coast and fall within the iSimangaliso Wetland Park, a World Heritage Site in the northern limits of the province of KwaZulu-Natal (Fig. 1). The region is also known as Maputaland and lies between neighbouring Swaziland and the coast, from Lake St Lucia to the Mozambican border. The reefs on which the coral communities are found are not true, accretive reefs since corals merely grow as a thin veneer on the limited Pleistocene sandstone substrata in the region (Ramsay and Mason, 1990; Ramsay, 1994, 1996; Cooper and Green, 2016). As coral reefs, they are thus marginal in nature and soft coral cover (~32%), comprising relatively few species (39), exceeds that of scleractinian cover (~27%; 93 species) over much of their surface (Schleyer, 2000; Celliers and Schleyer, 2008; Fig. 2). While not accretive, the coral communities nevertheless are rich in biodiversity at this latitude on the East African coast (Riegl, 1996a, b;

Schleyer, 2000; Schleyer and Celliers, 2003a, Schleyer and Celliers, 2005; Celliers and Schleyer, 2008), comprising a mix of tropical and subtropical species (Fig. 3). They are located at the south–western limits of the large Indo-West Pacific Marine Province (the ocean between the study area, the Red Sea and the Andaman Islands; Spalding et al., 2007) and, at a smaller biogeographic scale, they occur in the Delagoa Bioregion, which extends from Inhaca Island in southern Mozambique to Leven Point in South Africa (Porter et al., 2013; Fig. 1).

While they were discovered in 1970, intensive research only commenced on the reefs in 1990 and, in the following fifteen years, yielded publications on the geology (Ramsay, 1996) and biodiversity of the reefs (Riegl et al., 1995; Celliers and Schleyer, 2001, 2008; Schleyer, 2000; Schleyer and Celliers, 2005; Porter et al., 2013), many of which have been surveyed, mapped and zoned for potential use. Fundamental research has been undertaken on matters such as the local oceanography (Morris, 2009), coral systematics, distribution, reproduction and settlement (Riegl, 1996a, b; Benayahu and Schleyer, 1995, 1998;
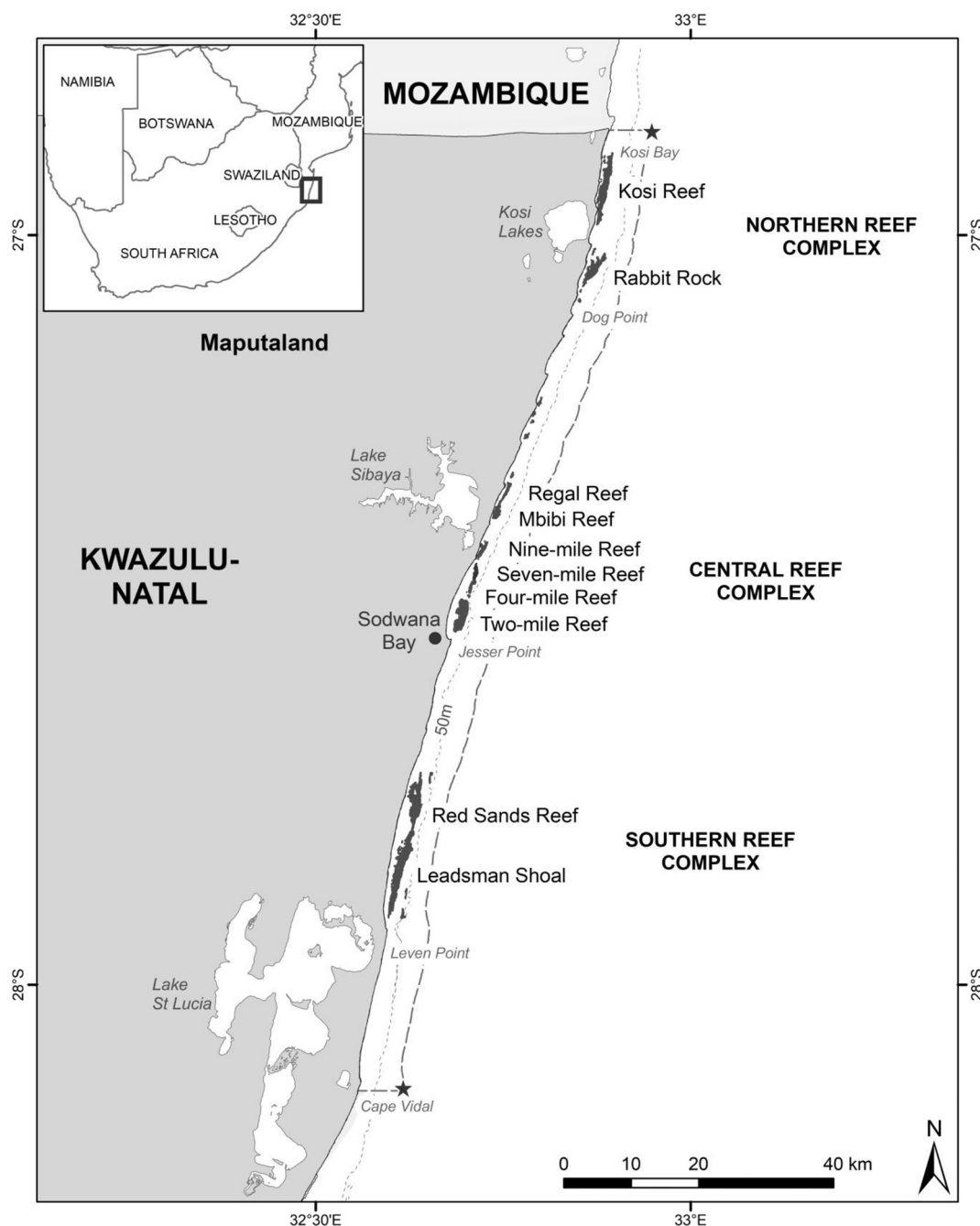
Fig. 1. Map of the Maputaland coast showing the major South African coral reefs within the marine boundaries (★) of the iSimangaliso Wetland Park.

Glassom et al., 2006; Monniot et al., 2001; Ofwegen and Schleyer, 1997; Kruger and Schleyer 1998; Kruger et al., 1998; Schleyer et al., 1997, 2003, 2004; Hart, 2018). Integrated monitoring was initiated early in the programme and yielded valuable information on coral community dynamics, climate-related bleaching and reef oceanography (Celliers and Schleyer, 2002; Morris, 2009; Schleyer and Celliers, 2003a, 2003b; Schleyer et al., 2005, 2008). Responses to factors such as crown-of-thorns starfish predation (Schleyer, 1998; Celliers and Schleyer, 2006), sedimentation (Riegl, 1995; Riegl and Branch, 1995; Schleyer and Celliers, 2003b) and recreational diving (Schleyer and Tomalin, 2000) were assessed, and studies on coral genetics (Macdonald, 2004) were initiated.

Comprehensive systematic studies have been published on the macro-algae in the iSimangaliso Wetland Park by the Universities of Cape Town and Ghent (104 species; Anderson et al., 2005) and limited

work has been undertaken on the taxonomy of the sponges (96 species; Schleyer and Celliers, 2003a, 2005; Samaai et al., 2010) and ascidians (30 species; Monniot et al., 2001; Schleyer and Celliers, 2003a). Mobile organisms are diverse and at least 314 invertebrate (Milne and Griffiths, 2014) and 399 fish species (Chater et al., 1993; Floros et al., 2012) have been recorded on the reefs. The deeper reefs and canyon margins have not been sampled as intensively but support distinct and diverse invertebrate communities and provide habitat for the coelacanth (Sink et al., 2006).

The above research has yielded background and baseline information on the reefs, their extent and condition. Climate change-related coral bleaching emerged globally as the greatest threat to coral reefs in the late 1990s but fortunately has not affected the Maputaland reefs to any great extent (Celliers and Schleyer, 2002; Schleyer and Celliers, 2003a; Porter et al., 2018). The potential of the Maputaland reefs to

Fig. 2. Wide-angle view of the abundance of soft corals typical of shallow, flat reef surfaces in Maputaland. Photo: Jerker Tamelander.

Fig. 3. View of typical Maputaland coral reef showing the rich biodiversity of tropical and subtropical species that grow as a veneer on the underlying rock substratum. Photo: Jerker Tamelander.

provide an early indication of climate change was nevertheless recognized in view of their marginal nature (Schleyer and Celliers, 2003a) and the effects of climate change became a major focus in subsequent research; we believe that the Maputaland reefs provide a model for the study of many of the stresses to which these valuable coral systems are being subjected globally.

The ensuing paper thus reviews the results of relevant studies conducted over the past decade, the purpose of which was to elucidate, as far as possible, the biological and human consequences of climate change on south east African coral reefs. In this regard, it updates earlier premises presented on the subject by Schleyer and Celliers (2003a, 2003b).

2. Regional oceanography

The Maputaland coastline is straight and exposed (Fig. 1) and, as the prevailing north-easterly and southerly to south-westerly winds blow parallel to the coast, they give rise to substantial swells (Fig. 4). The warm Agulhas Current has a mean peak velocity of 1.4 m/s (Lutjeharms and de Ruijter, 1996) and flows in a south-westerly direction along the coast, generating sub-tropical conditions in the area. This current is the most powerful western boundary current in the southern hemisphere and develops around 27°S, just south of the border between South Africa and Mozambique (Lutjeharms, 2006). It is essentially in its infancy off Maputaland and is subjected to anomalous mesoscale influences from its source waters that emanate from the South West Indian Ocean (Braby et al., 2016). These anomalies include mesoscale eddies, both cyclonic and anticyclonic, propagating southwards through the Mozambique Channel (Ternon et al., 2014), and as dipole features flowing westward across the southern Mozambique Channel; the latter are formed as the South East Madagascar Current terminates south of Madagascar (Ridderinkhof et al., 2013). A continuous flow of the Mozambique Current may occur along the shelf edge of the African mainland on rare occasions (~once a year) and for only short periods (~9 days), but could provide transport for biota to traverse the length of the Mozambique coast (Lutjeharms et al., 2012). Potential connectivity of this nature, as well as across the Mozambique Channel in its northern reaches to Madagascar, has recently been demonstrated in a particle transport model (Schleyer et al., submitted).

De Ruijter et al. (2004) undertook an opportunistic survey of a dipole formed off the south of Madagascar and determined that such features are deep, energetic, and similarly capable of transporting water
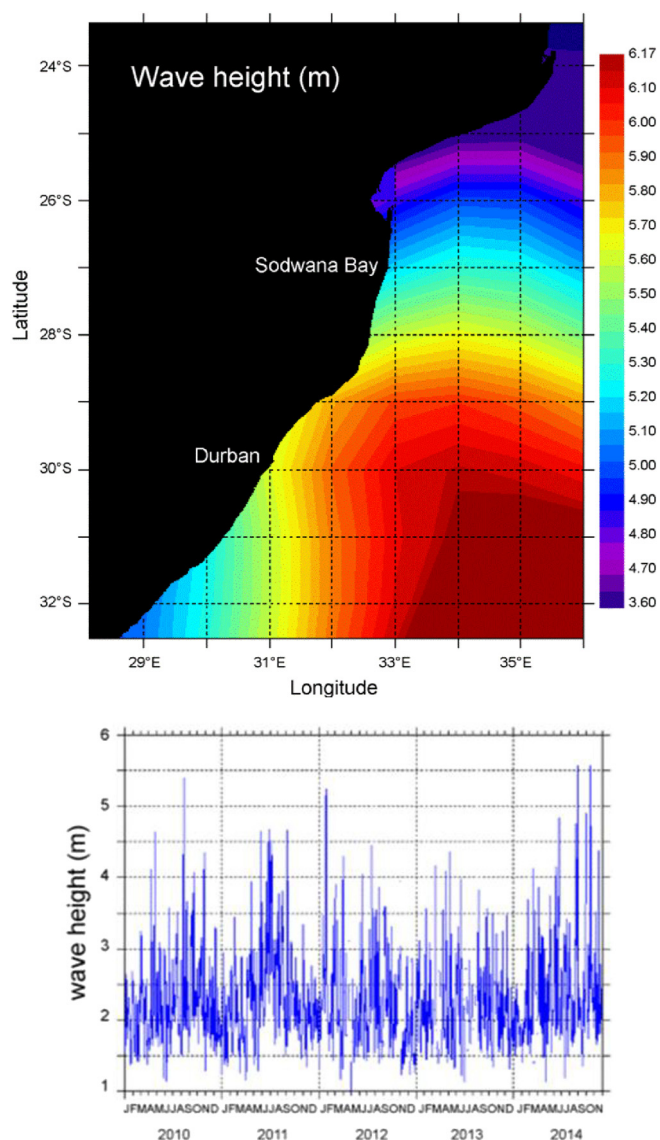
Fig. 4. South Africa's east coast is subjected to large swells (top) that generate waves of significant height on the Maputaland reefs (bottom). Both show significant wave height (the average of the highest one-third of waves) in a given period, the top being for a 24 h period on 31 August 2014 at 0.33° resolution, the bottom being a time-series of significant wave heights at 24 h intervals for Sodwana Bay from January 2010 to November 2014.

masses across the Mozambique Channel. Morris' (2009) results, combined with detailed analyses of 18 years of sea surface altimetry data, showed that between four and six of these features traverse the southern Mozambique Channel each year (Ridderinkhof et al., 2013). Using high resolution modelling, Halo et al. (2014) further showed that cyclonic eddies spawned off south-west Madagascar are the longest-lived eddies to travel across the channel, persisting for over 100 days, and thus capable of reaching the northern KwaZulu-Natal shelf region. The aforementioned particle transport model has also demonstrated potential connectivity from Madagascar to Mozambique, but to a lesser degree due to a slower passage (Schleyer et al., submitted).

Mean seasonal sea surface temperatures (SST) in the Maputaland region range from 22 °C in winter to 26 °C in summer (SADCO data, 1960–1995), with a salinity range of 35.0–35.5 PSU (Schumann and Orren, 1980). Since the shelf is narrow and lacks any significant riverine input, the region is bathed in the clear oligotrophic oceanic water of the Agulhas Current, derived from the Mozambique Channel and South-East Madagascar Current (Lutjeharms et al., 2012; Porter et al.,

2017a). Chlorophyll, turbidity and nutrient levels are thus relatively low compared to adjacent regions and temperatures on the reefs average 24.4 °C (Porter et al., 2017a; Porter and Schleyer, 2017). This despite the fact that cyclonic eddies generated along the western boundary of the Agulhas Current can cause upwelling of cooler water on the reefs (Lutjeharms, 2006; Morris, 2009).The maximum tidal flux is 2 m during spring tides, dropping to 1 m during neap tides.

3. Oceanographic influences at Sodwana Bay

The question arises as to how mesoscale features emanating from the north and east affect the northern KwaZulu-Natal shelf and, in turn the coral reefs found along the Maputaland shelf region? On examination of surface drifter data, an eddy tracking scheme and satellite-derived geostrophic currents, Braby et al. (2016) found that mesoscale cyclonic and anticyclonic eddies move in to northern KwaZulu-Natal waters fairly regularly, but that they dissipate within ± 100 km of entering the Agulhas Current. Anticyclonic eddies were further shown to increase the velocity of the Agulhas Current by 0.16 ± 0.17 m/s, while cyclonic eddies were shown to decrease the Agulhas Current velocity by 0.13 ± 0.16 m/s and divert it up to 144.73 ± 84.98 km offshore (Braby et al., 2016).

Morris et al. (2013) surveyed a cyclonic eddy offshore and to the north of Sodwana Bay, flanked by two anticyclonic eddies to the north and south (Fig. 5a). Once the cyclonic eddy, interacted with the shelf, it induced a prolonged cooling event, which was recorded on a long-term monitoring temperature sensor deployed in 18 m of water at Nine-mile Reef at Sodwana Bay. Furthermore, interaction between the cyclonic eddy and the anticyclonic eddy to the north caused an even more intense upwelling event as they propagated southwards over the shelf edge. Based on the Nine-mile Reef temperature data, between two and five cyclonic eddies per year influence the shelf edge, either in direct consequence of dynamic uplift associated with cyclonic eddies, or by interaction with anticyclonic eddies, causing divergent upwelling events (Morris et al., 2013). Examples of these interactions are shown in Fig. 5b.

Mesoscale eddies are not the only anomalous features to affect the shelf region in northern KwaZulu-Natal. Submarine canyons of varying maturity that intrude onto the shelf (Ramsay and Miller, 2006; Green, 2009) provide avenues for the penetration of cold, nutrient-rich waters to some of the coral reefs (Morris, 2009). Analysis of temperature records from sensors located at the head of one such canyon, Wright Canyon at Four-mile Reef, reveals that the canyon head is cooler year-round with sharp decreases in temperature that are probably associated with the southward flow of the Agulhas Current (Morris, 2009).

4. Study reefs

The major coral-inhabited reefs in KwaZulu-Natal lie adjacent to the coast from 26°50′S to 27°55′S (Fig. 1) and are a mere 40 km² in extent. They are among the southernmost coral reefs in the world but are not typical of coral reefs resulting from biogenic accretion. As early as 1999, it was recognized that relatively low temperatures and aragonite saturation combined with a high-latitude low photoperiod, particularly in winter, are limiting factors for reef development (Kleypas et al., 1999). The Maputaland reefs are consequently non-accretive and Kleypas et al. (1999) considered them marginal 'non-reefs'. Corals in South Africa thus form a veneer of this life-form on late Pleistocene sandstone, originating from submerged coastal sand dunes (Ramsay and Mason, 1990; Ramsay, 1996). As a result, the reefs run parallel to the coastline and are confined to the narrow continental shelf (2–7 km; Martin and Flemming, 1998). They are conveniently grouped into a northern, central and southern complex by Riegl et al. (1995), these being respectively found at Kosi Bay, between Sodwana Bay and Lake Sibaya, and north of Lake St Lucia (Fig. 1). Extensive sandy substrata separate the individual reefs and complexes. Submerged canyons
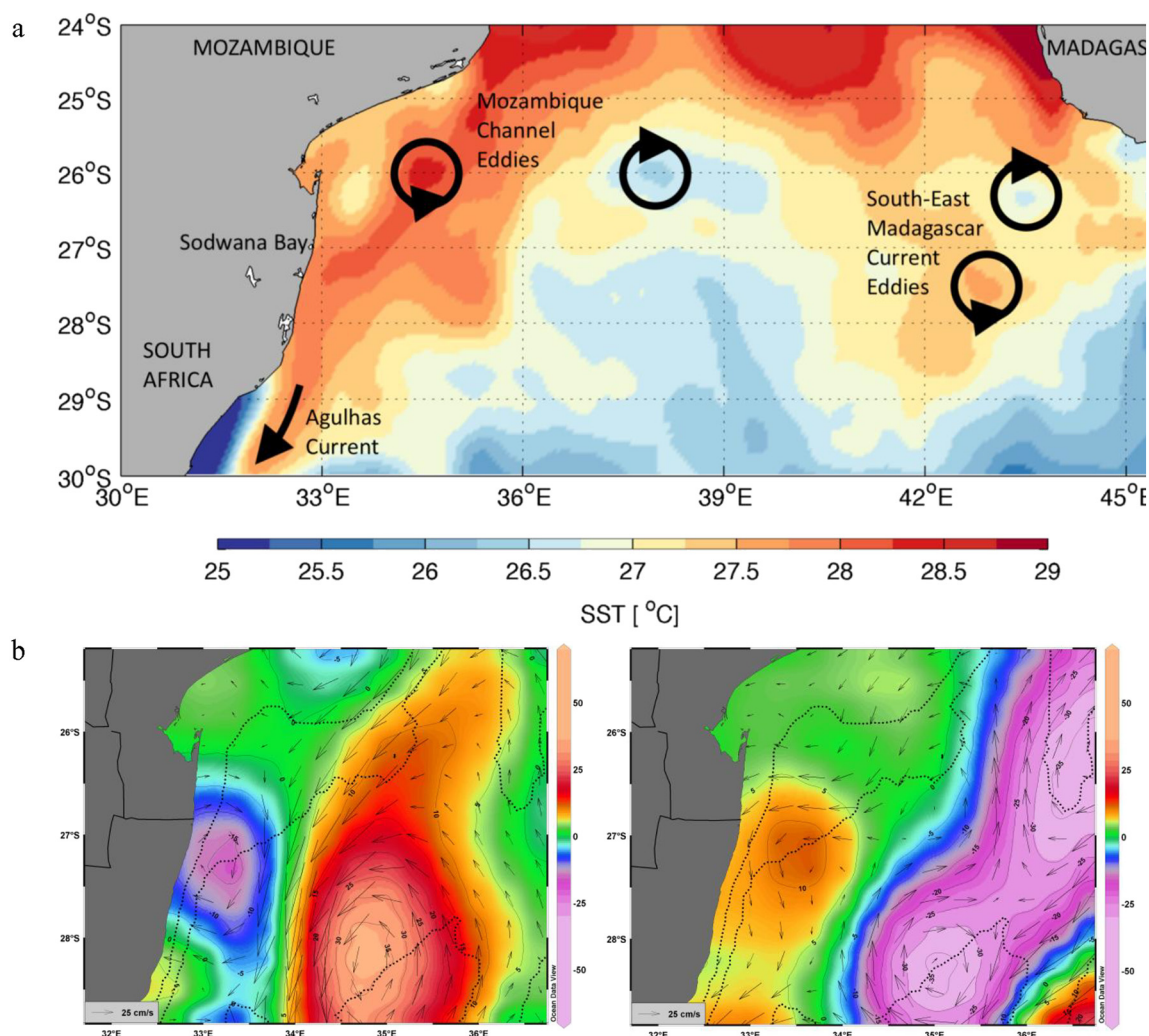
Fig. 5. a) Sea surface temperature image of the southern Mozambique Channel region (OSTIA 5 km resolution – 3 March 2016), with mesoscale eddies emanating from the Mozambique Channel and South-East Madagascar Current depicted as source waters of the Agulhas Current; b) a cyclonic (left) and anti-cyclonic eddy (right) interacting with the northern KwaZulu-Natal coastline.

penetrate the shelf adjacent to some of the reefs in the central reef complex, and immediately to the south of the southern reef complex (Ramsay and Miller, 2006; Green, 2009).

The central reef complex has received the most attention, being the most accessible, but the reefs are all essentially physiognomically similar in structure. They lack the well-defined zonation of true coral reefs and conform to the topography of the base substratum (Fig. 3), ranging in depth from 8 to 30 m. They tend to be flat with relatively few features comprising low pinnacles and shallow drop-offs and gullies. Riegl et al. (1995) broadly categorised the coral communities into reef top and gulley communities on biological grounds. The former are dominated by soft corals, while hard corals attain a greater abundance in the latter. Celliers and Schleyer (2008) later statistically determined that there were eight discreet communities in the central reef complex, and Schleyer and Porter (in press) refined this further, correlating coral community distribution on all the South African coral reefs with important abiotic derived from reef survey data. Latitude proved to be the strongest predictor of the distribution of 42 definable coral reef communities on the Maputaland reefs, with depth, slope, turbulence and reef aspect playing a diminishing role in that order.

5. Reef processes

The most important large-scale determinants of coral community

structure in the Western Indian Ocean appear to be temperature and wave-generated turbulence, as well as low levels of fluvial turbidity (Porter et al., 2014, 2017a). The role of temperature in the Delagoa Bioregion is dealt with in depth in the following section on long-term monitoring. Wave action is thought to be fundamentally important over large scales as it may retard more delicately branched acroporids and other structurally complex reef-building corals from proliferating, and favour encrusting growth forms of soft corals, particularly on the shallow reaches of the reefs (Schleyer, 2000; Porter et al., 2017a). Furthermore, it mobilises sediment, particularly in sand-filled gullies where sediment-tolerant Alcyoniidae of the genera *Lobophytum* and *Sarcophyton* are notably abundant (Schleyer and Celliers, 2003a, 2003b).

Coral damage due to episodic storms has been related to differences in community structure on the reefs (Riegl and Riegl, 1996). High-energy wave-events that occur with regularity (Fig. 4) may stunt hard coral colonies to such an extent that reef framework can neither be built or maintained (Riegl, 2001), a disturbance considered in their conservation management (Celliers and Schleyer, 2008). Although the reefs lie distant from the tropical cyclone belt ~500 km to the north in the Mozambique Channel, they nevertheless experience cyclone-generated and Southern Ocean swells, which has resulted in coral-growth forms that can tolerate this high energy environment (Riegl, 2003). The frequency and intensity of cyclones, and possibly their southward

migration, is predicted to increase with climate change (Webster et al., 2005).

Key small-scale, reef-level determinants of community composition are depth, reef physiognomy and sedimentation (Porter et al., 2013, 2017a, 2017b; Schleyer and Celliers, 2003a, 2003b; Schleyer and Porter, in press). There are clear differences in community composition between shallow (< 10 m), mid-depth (~15 m) and deep reef (~30 m) communities (Riegl et al., 1995; Porter et al., 2013, 2017a; Schleyer and Celliers, 2003a, 2003b). Riegl et al. (1995) found that coral communities residing at 10–15 m tended to be dominated by soft corals, whereas deeper reefs (15–20 m) are more scleractinian-dominated. The role of depth in structuring communities may be a surrogate for the synergistic effects of wave-generated turbulence and light attenuation.

Particulate pollution is low on these reefs and chemical pollution is also thought to be low due to turbulence on the reefs and the lack of fluvial and industry input. However, recent work has shown that many reef organisms, particularly long-lived species, have significantly high levels of organochlorine pesticide residues in their tissues, including DDT (Porter et al., submitted). *Sinularia gravis* on the Mbibi and Red Sands reefs was found, in particular, to have total organochlorine pesticide levels of up to $3 \mu g.g^{-1}$ (wet wt). Isotopic evidence suggests that groundwater, laden with pesticides of terrestrial origin from large coastal lakes and wetlands, is supplying these pollutants (Porter et al., submitted). At this stage it is unclear what effect these pollutants may be having on the coral communities, but they are being investigated as a possible cause for the changes in coral cover measured over the past 25 years (Porter and Schleyer, 2017).

6. Long-term monitoring

Long-term monitoring of the reefs commenced in 1993 when a fixed monitoring site was established on Nine-mile Reef at Sodwana Bay, entailing annual photo-quadrat surveys and hourly temperature logging

(Fig. 6). Dynamics in reef cover, coral mortality and recruitment success have been assessed to establish the effects, if any, of climate change (Schleyer et al., 2008; Porter and Schleyer, 2017). Although sea temperatures rose by 0.15 °C p.a. at the site up to 2000, they have subsequently been decreasing, and the overall trend, based on monthly means, has been a significant decrease of 0.03 °C p.a. (Fig. 6a). Despite this, minor bleaching was encountered in the region during the 1998 El Nino Southern Oscillation event, again in the summer of 2000–2001 (Celliers and Schleyer, 2002), in 2005 and in 2016 (Porter et al., 2018); the coral bleaching threshold on the reefs was estimated to be in the region of 28.5 °C (Celliers and Schleyer, 2002). A significant decreasing trend of 0.95% p.a. in soft coral cover (from 58% in 1993 to 38% in 2014) has been evident throughout the monitoring period (Fig. 6b), attributable to significant decreases in *Sinularia* and *Lobophytum* spp. cover. Contrastingly, hard coral cover gradually and significantly increased by 6% up to 2005 (Fig. 6b), this being largely attributable to increases in cover by *Acropora* spp. Recruitment success and mortality in both the soft and hard corals has displayed high inter- annual variability, with increasing but non-significant trends in the last five years (Porter and Schleyer, 2017).

While the reduction in soft coral cover has been more consistent and greater than the increase in hard corals, it is difficult at this stage to attribute the former to changes in water quality, acidification-linked accretion, temperature or the aforementioned pesticide levels. Regional decadal patterns in temperature, however, do show a long-term increase in temperature according to Reynolds sea surface temperatures (Schleyer et al., 2008).

Distributional changes can be expected in the coral community if temperatures increase, with more tropical species gradually appearing on the South African coral reefs and temperate species being gradually displaced southwards. Examples of this have been observed: Floros et al. (2012) recently published a new record of *Acropora robusta*, common further north, on the South African reefs; and it has been
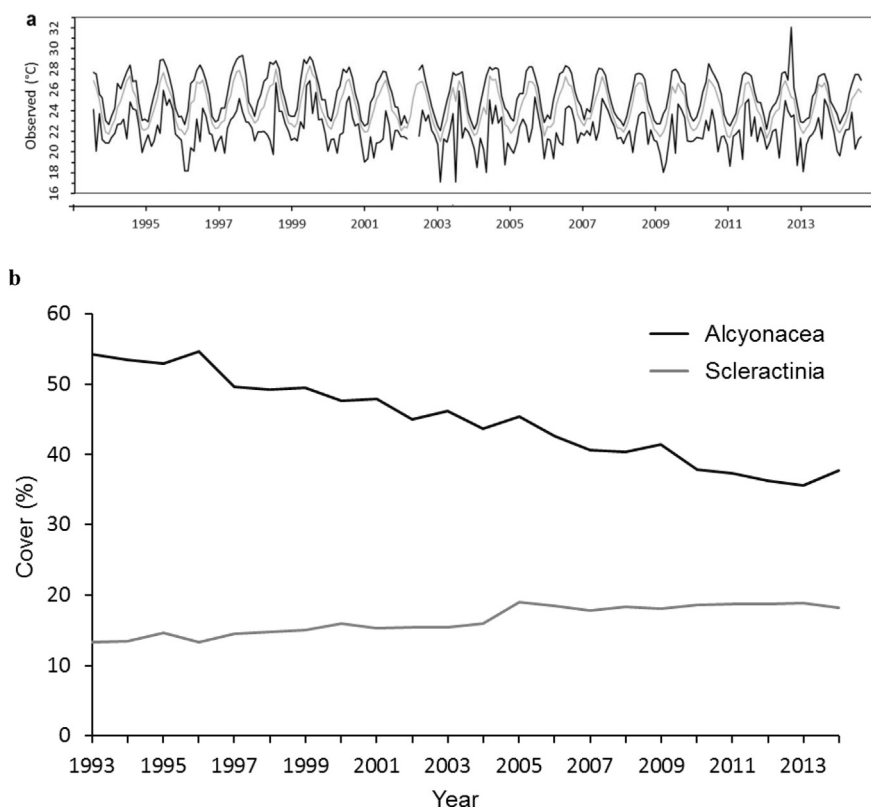

Fig. 6. Monthly mean, maximum and minimum temperatures recorded at 18 m at a long-term monitoring site at Nine-mile Reef, Sodwana Bay, and trends in alcyonacean and scleractinian cover.

observed that *Eleutherobia aurea*, which was found in limited numbers on the deeper Sodwana Reefs but is common further south (Benayahu and Schleyer, 1995), no longer appears to occur there (Schleyer, unpub. data).

7. Genetic connectivity

Coral reproduction and reef connectivity are of particular interest on marginal, discontinuous reefs faced with climate change, such as those found in Maputaland. Early research demonstrated reproduction in both soft and hard corals (Kruger and Schleyer, 1998; Kruger et al., 1998; Schleyer et al., 2004) and these studies were expanded to include the fast-growing scleractinian, *Acropora austera*, and the slow-growing, massive corals, *Platygyra daedalea* and *Hydnophora exesa* (Massé, 2014; Hart, 2018) in which normal reproduction was encountered. These species were selected as a 'hare' and as 'tortoises' for this and other studies to exemplify the different life strategies employed by fast and slow growing corals under our conditions. In a similar context, our early genetic research on connectivity targeted *Stylophora pistillata*, which is widely distributed but not ubiquitous on South African coral reefs. While widely divergent in morphology, it was found to comprise a single species (Macdonald, 2004). Genetic connectivity studies were subsequently extended to *A. austera* and *P. daedalea* (Macdonald et al., 2010, Macdonald et al., 2009, 2010; Montoya-Maya, 2013, Montoya-Maya et al., 2014a, b, Montoya-Maya et al., 2016) and the results are presented in a regional context.

The ecologically relevant (one or two generation) connectivity of *A. austera* and *P. daedalea* was assessed between and within the Maputaland reefs as well as the Chagos Archipelago, Reunion Island, and Bazaruto Island and Pemba in Mozambique using hyper-variable genetic markers. Six microsatellite loci were amplified in *A. austera* and five in *P. daedalea* using primers and protocols described by Montoya-Maya et al. (2014a; *A. austera*) and Miller and Howard (2003; *P. daedalea*). Three nuclear intron markers were also genotyped and multi-locus genotypes (MLGs) were constructed for each coral sample collected by combining nuclear data from the intron and microsatellite loci (Montoya-Maya et al., 2016).

The analysis of genetic diversity and differentiation between reefs provided evidence for the existence of four discrete genetic populations of *A. austera* and five of *P. daedalea* in the region (Fig. 7). The highest genetic diversity and most private alleles were found on Nine-mile Reef, the northernmost reef in the Central Reef Complex, and at Rabbit Rock, which suggests these reefs play a role as sinks for putative migrants. Assignment tests that identified migrants to the South African coral reefs left some individuals unassigned, but assigned the greatest proportion of putative recruits to their source reef, providing evidence of high levels of self-seeding (and also of an unsampled, source population). Together, the data indicate that South African coral populations are, at ecological time scales, independent of gene flow from more distant coral populations. The spatial arrangement of the regional patterns were similar in both coral species (Fig. 7) and are in agreement with those in other benthic species (i.e. mangrove crab *Perisesarma guttatum*, Silva et al., 2010; sea urchins *Tripneustes* spp., Lessios et al., 2003; mud crab *Scylla serrata*, Fratini and Vannini, 2002). All these studies indicate that genetic panmixia cannot be assumed in southern African benthic marine invertebrates.

Intensive, geo-referenced sampling at the reefal scale (within-reef) revealed genetic discontinuity in both species, providing further corroborative evidence of genetic partitioning in the region. Two (*P. daedalea*) to four (*A. austera*) clusters of these coral species were identified on Two-Mile Reef (TMR) and may be related to the neighbourhood sizes of each species (Fig. 8). The clusters were genetically distinct, particularly in the case of *A. austera* but less so in *P. daedalea*. Similarly, there was evidence of Spatial Genetic Structure (SGS), indicative of non-random or limited dispersal in *A. austera* (Fig. 9); the evidence for this in *P. daedalea* was statistically inconclusive. More importantly, there was significant relatedness between closely-spaced individuals of *A. austera* and the hierarchical partitioning analysis suggested that dispersal of this species was non-random and resulted from specific larval settlement preferences (e.g. the presence of adults or depth and location), not only water movement (Table 1). Thus, the findings suggest that, at least for *A. austera*, the dispersal of larvae might be limited to as little as a couple of tens of meters on TMR. This altogether challenges the assumption that the larvae of such corals are passive in their
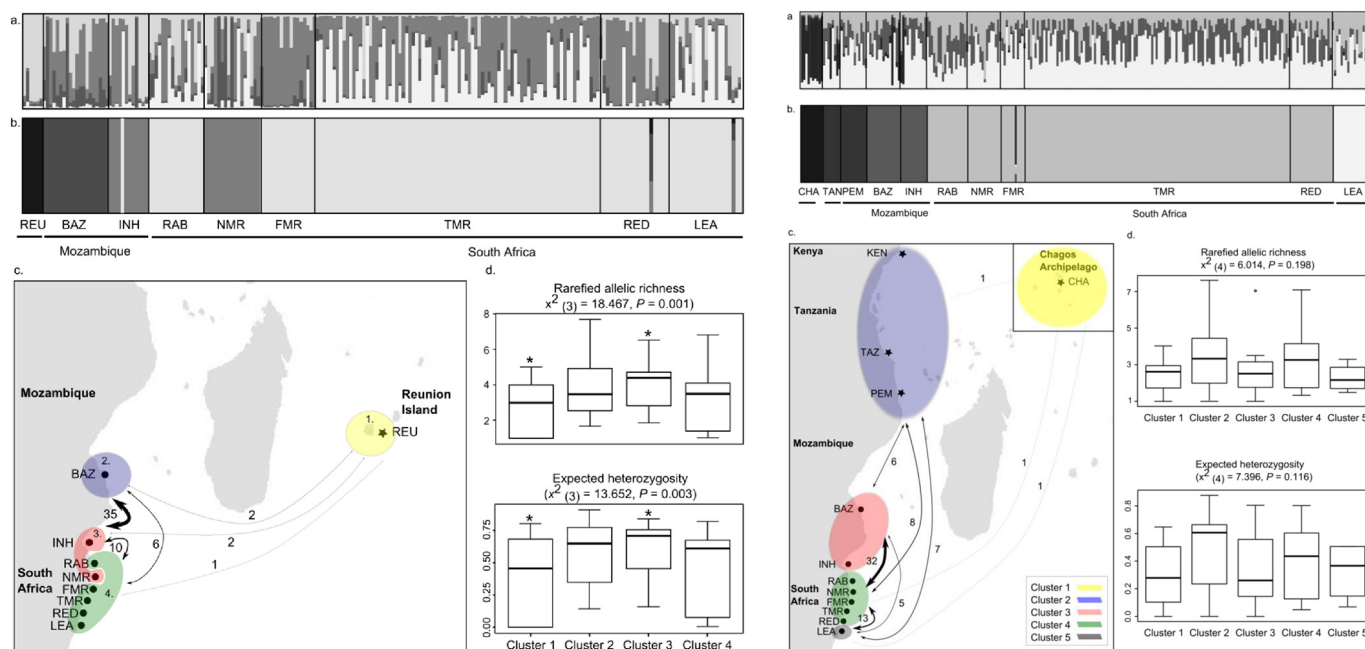

Fig. 7. Between-reef genetic structure of *Acropora austera* (left) and *Platygyra daedalea* (right) along the south-east African coast estimated by Bayesian clustering analysis. Clusters identified by Structure (a) and by BAPS (b). Shown in (c) are long-term gene flow (arrows) and estimated number of migrants per generation (N_em, numbers) between clusters (numbered and coloured areas) identified by BAPS. Box plots (d) depict the distribution of genetic diversity in each cluster; thick lines correspond to the median and whiskers represent the interquartile range. * = Significant pairwise differences after FDR.
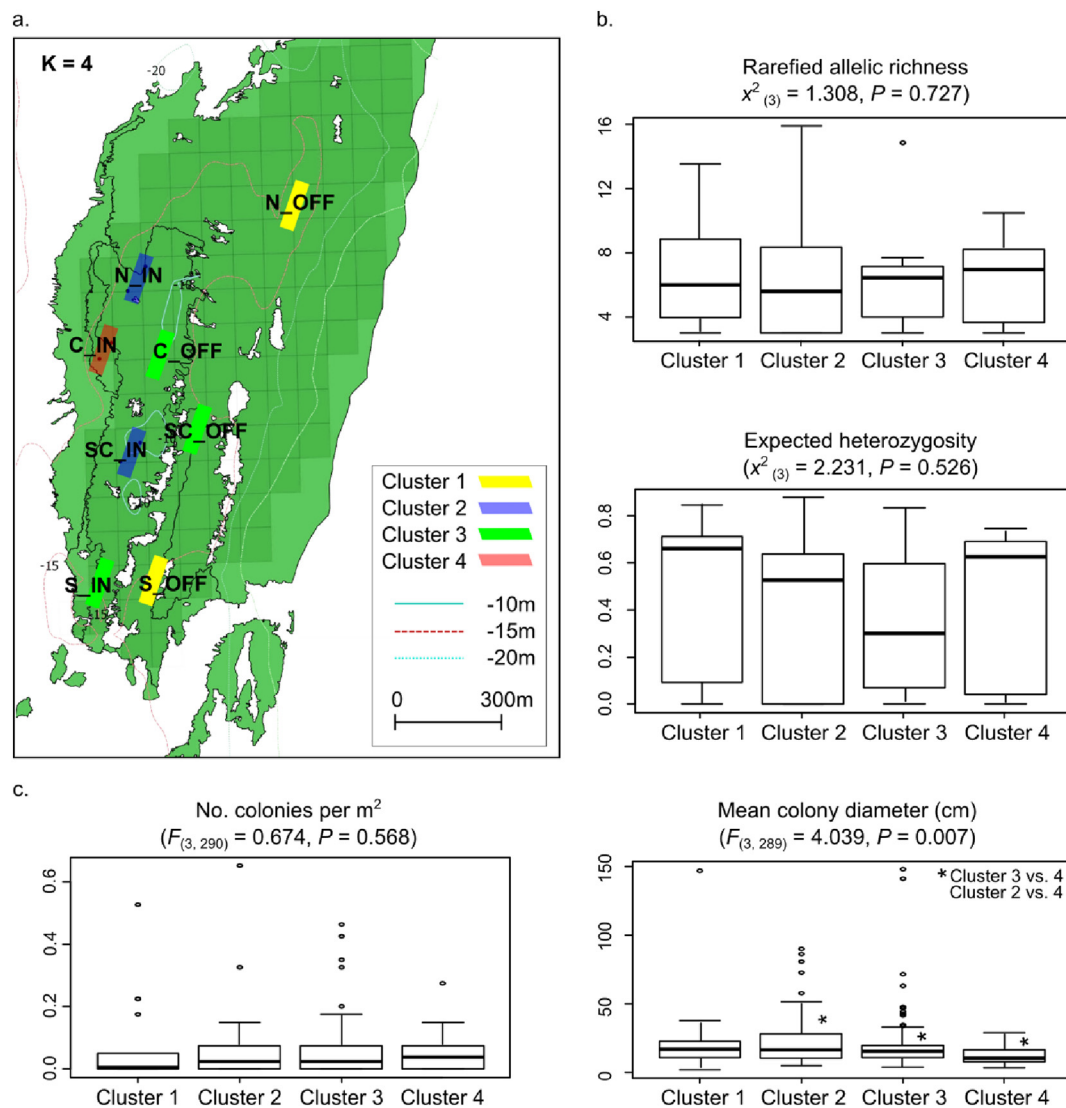
Fig. 8. Within-reef population structure of genetic populations of *Acropora austera* on TMR suggested by Bayesian spatial clustering of groups implemented in BAPS: a) labels correspond to the sampling sites and colours to clusters; box plots depict the distribution of genetic diversity (b) and population demographics (c) between clusters; thick lines correspond to the median and whiskers represent the interquartile range. * = Significant pairwise differences after FDR.

movement.

The results clearly suggest that there is demographic discontinuity between the coral populations along the south-east African coast, a finding consistent with isolation observed in other studies using less variable markers. More importantly, *Acropora austera* and *P. daedalea* represent different life strategies in the South African coral communities, yet manifested similar genetic patterns, suggesting that these corals are responding similarly to forces that are driving genetic connectivity in the region. For management purposes, the genetically distinct populations identified at each of the spatial scales analysed in this

study may thus correspond to management units, or evolutionarily significant units. Furthermore, some reefs appear to act as 'landing-sites' for migrants (Nine-mile Reef and Rabbit Rock) and adaptive management should be employed in the conservation of the reefs in the region.

8. Coral diseases

While coral bleaching has received considerable attention since the 1998 El Nino Southern Oscillation (ENSO) that resulted in 50–60%
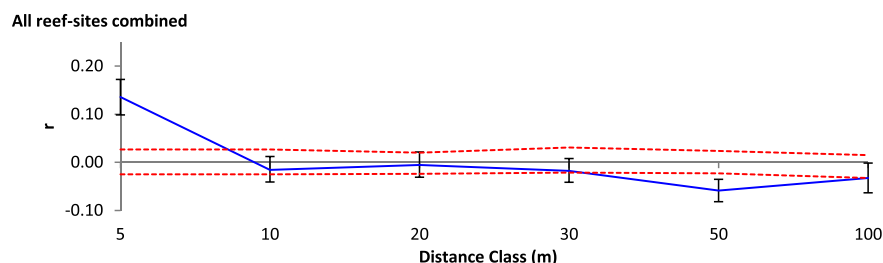

Fig. 9. Spatial autocorrelation plots of *Acropora austera* on TMR derived from GenAlEx depicting the individual-by-individual pairwise relatedness as a function of distance. Dashed lines represent the 95% confidence intervals of a null hypothesis of no autocorrelation in 9999 permutations, and error bars delineate standard errors from jack-knifed estimates.

Table 1

Hierarchical partitioning of genetic variation in *Acropora austera* on TMR: I% = the percentage variance explained by individual variables, I = variance explained by individual variables, J = variance explained together with other variables, Total = the total variance and Z = the score from the randomization procedure. Variables in bold are significant based on randomization (Z ≥ 1.65) and the 95% confidence limit. The bootstrapped Pearson correlation coefficient (rP) and its 95% confidence interval (CI) are also provided.

Variable	I%	I	J	Total	Z	rP	95% CI
Local FST							
Mean colony size	24.043	1.726	−1.541	0.185	0.160	−0.213	(−0.327,0.825)
Density	18.887	1.356	−0.572	0.784	0.190		
Location	49.818	3.577	−2.692	0.886	2.300	−0.446	(−0.968,0.416)
Latitude	0.957	0.069	−0.025	0.043	−1.000		
Depth	6.295	0.452	−0.446	0.006	−0.790		
Local r							
Mean colony size	10.330	0.776	1.069	1.845	−0.060		
Density	54.652	4.105	−0.467	3.638	2.240	0.733	(0.035,0.988)
Location	5.943	0.446	0.581	1.028	−0.540		
Latitude	17.149	1.288	−1.035	0.253	−0.330		
Depth	11.926	0.896	0.184	1.080	−0.330		

mortality in the Western Indian Ocean (Obura, 2005), very little attention has been given to coral diseases (McClanahan et al., 2004) that are often associated with the phenomenon. A study was thus undertaken to investigate the prevalence and variability of coral diseases on Two-mile Reef and determine their seasonal variation and spatial distribution.

The surveys were conducted at seven sites along a north-south gradient on Two-mile Reef at 8–10 m (shallow inshore region) and 12–16 m (deeper offshore region). Scleractinian corals were recorded to genus level, as well as colonies manifesting disease, bleaching or necrosis, within five 10 × 2 m transects at each site. The surveys were conducted over two consecutive austral summers and winters in 2011 and 2012 to gain a measure of seasonality in the prevalence of the diseases (Table 2).

Gross lesions observed during the surveys were photographed and identified, primarily using the Underwater Cards for Assessing Coral Health on Caribbean and Indo-Pacific Reefs (Beeden et al., 2008). Coral genera exhibiting comparable gross lesions were considered to have the same disease (e.g. BBD, WS, etc.). Since similar lesions can be manifested by multiple microscopic pathologies caused by different agents (Work and Rameyer, 2005), samples of each coral disease were also collected and described according to the nomenclature developed by Work and Aeby (2006). Disease prevalence, calculated per transect, was averaged for each site and the overall prevalence was expressed as a proportion of the total infected coral colonies. The observed disease prevalence of coral genera was also compared with their expected susceptibility according to their abundance in the field (Aeby et al., 2010, 2011).

The surveys revealed the presence of six main coral diseases (Fig. 10), viz. white syndrome (WS), black band disease (BBD), skeleton eroding band (SEB), pink line syndrome (PLS), growth anomaly (GA) and *Porites* white patch syndrome (PWPS; Séré et al., 2012, 2013). Their overall prevalence was variable between the survey periods (Table 2), with a higher average prevalence in 2012 (4.9 ± 0.9%; mean ± SE) than 2011 (2.9 ± 0.8%; mean ± SE). The most common disease was WS; the prevalence of the others was much lower (Table 3). Since PWPS

Table 2

Mean coral disease prevalence (± SD) at Sodwana Bay during successive winters and summers in 2011–2012.

Period/dates	Season	Prevalence
February 2011	Summer 1	3.9 (3.6)
July 2011	Winter 1	1.9 (1.2)
February 2012	Summer 2	4.1 (2.0)
June 2012	Winter 2	5.7 (3.2)
Total		3.9 (1.1)

constituted a newly-described condition (Séré et al., 2012), it was accorded attention in terms of its aetiology (Séré et al., 2013) and the causative organism was isolated as *Vibrio tubiashii* (Séré et al., 2015a).

A total of seven scleractinian coral genera were observed with signs of disease (Fig. 10; Table 4), the most susceptible being *Astreopora*, *Hydnophora*, *Pocillopora* and *Porites*. While these coral genera varied in their disease susceptibility, no clear relationship was found between their abundance and disease prevalence. These genera are commonly found in both the shallow inshore and deeper offshore regions of TMR, and are important reef-building corals in the Western Indian Ocean (Turner and Klaus, 2005). Massive colonies of *Porites lutea* and *P. lobata*, generally considered robust and slow-growing (Raymundo et al., 2005), were prone to multiple infections, but exhibited mainly signs of PLS and PWPS. *Hydnophora* spp. comprise a minor component in South African coral communities (Table 4) and exhibited a particularly high susceptibility to BBD and WS. *Astreopora*, represented by the species *A.myriopthalma*, manifested signs of GA, WS, CT and BBD. Colonies of *Pocillopora* spp. exhibited high susceptibility to WS, particularly in the shallow reef zone (Table 4).

All the coral diseases recorded during this study have been previously reported at other localities across the Indian Ocean, including Reunion and Mayotte (Séré et al., 2015b), the Chagos Archipelago (Sheppard et al., 2012), Republic of Maldives (Onton et al., 2011), South India (Thinesh et al., 2009, 2011), and generally within the Indo-Pacific region (Willis et al., 2004; Raymundo et al., 2005; Aeby et al., 2006). The average disease prevalence at Sodwana Bay was higher than that found at Mayotte (2.7%; Séré et al., 2015a) and at other Indian Ocean localities such as Ningaloo Reef in Australia (2.3%; Onton et al., 2011) and the Maldives (< 2%; Montano et al., 2012). However, the values obtained were substantially lower than those recorded at Reunion (7.5%; Séré et al., 2015a), the Chagos Archipelago (5.2%; Sheppard et al., 2012), Palk Bay (21.0%; Thinesh et al., 2011) and Mandapam (8.9%; Thinesh et al., 2009) in South India.

Seasonally, WS was more prevalent on *Acropora* and *Pocillopora* colonies in summer than winter. A similar seasonal trend appeared evident for PWPS but the differences between summer and winter were not significant. Spatial variability was detected in both BBD and WS on Sodwana Bay reefs, these being more abundant on shallower depths, a trend consistent with patterns found in the Caribbean (Weil and Cróquer, 2008), Republic of Maldives (Montano et al., 2012) and South India (Thinesh et al., 2009, 2011).

A higher prevalence of disease was evident in the 2011 summer at Sodwana Bay and appeared to be linked to warmer water temperatures. This was the case for WS-infected *Acropora* spp. and *Pocillopora* spp. However, no variations were observed for this syndrome between the summer and winter of 2012. PWPS also appeared more prevalent on both the reef slope and reef flat in summer but the results were not
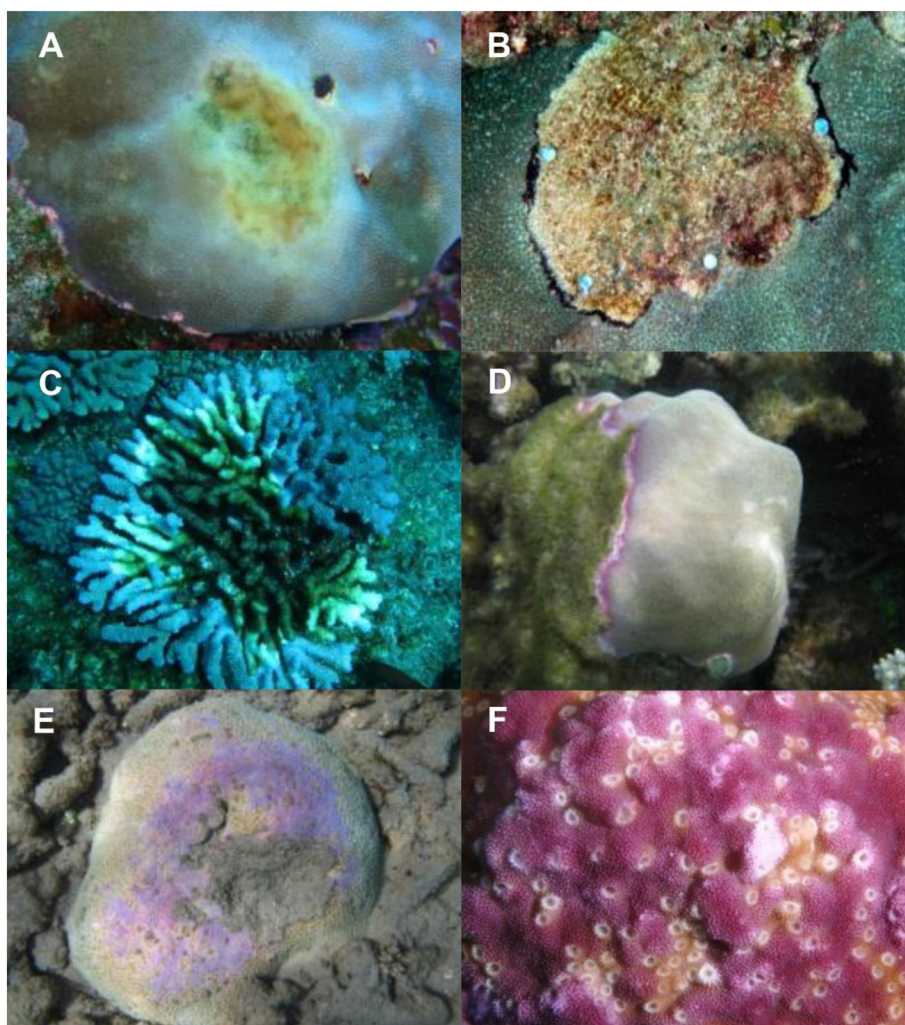
Fig. 10. Main coral diseases observed at Sodwana Bay: A) *Porites* white patch syndrome (PWPS) on *Porites lutea*; B) active black band disease (BBD) on *Goniopora djiboutiensis*; C) white syndrome (WS) on *Acropora* sp.; D) pink line syndrome (PLS) on *Porites lobata*; E) compromised tissue (CT) on *Astreopora* sp.; F) growth anomalies (GA) on *Astreopora myriophthalma*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Overall prevalence (the number of diseased coral colonies divided by the total number of colonies identified to the genus level within each transect; ± SE) of the main coral diseases in coral genera at Sodwana Bay (n = 17,140 coral colonies) between 2010 and 2012.

Disease	Prevalence
Bleaching	0.4 (1.3)
White syndrome (WS)	2.1 (2.5)
Pink line syndrome (PLS)	0.5 (0.9)
Porites white patch syndrome (PWPS)	0.2 (0.5)
Black band disease (BBD)	0.4 (0.6)
Compromised tissue (CT)	0.8 (0.3)
Growth anomaly (GA)	0.1 (0.5)
Skeletal eroding band (SEB)	–
Σ disease	3.9 (0.8)

Table 4

Relative abundance (% ± SE) of the main coral genera manifesting disease and mean prevalence (% ± SD) of all diseases calculated relative to the total number of colonies in the respective genera at Sodwana Bay.

Genera	Shallow inshore region		Deeper offshore region	
	Host abundance	Prevalence	Host abundance	Prevalence
Acropora	23.8 (21.4)	4.1 (4.2)	23.0 (30.5)	2.7 (2.9)
Astreopora	2.3 (4.5)	5.8 (5.5)	3.0 (4.1)	10.9 (7.1)
Hydnophora	1.8 (3.4)	11.9 (10.8)	2.0 (2.5)	13.4 (15.4)
Montipora	11.2 (7.9)	0.5 (0.9)	14.6 (13.9)	2.6 (2.7)
Platygyra	5.7 (6.6)	2.0 (2.3)	4.1 (4.5)	0.2 (0.3)
Pocillopora	18.0 (15.9)	16.4 (14.0)	8.9 (9.1)	8.2 (6.1)
Porites	4.4 (4.5)	22.4 (18.8)	4.0 (3.0)	12.0 (11.6)

statistically significant. Similar seasonal patterns have been reported for both BBD and WS in Australia (Willis et al., 2004; Page and Willis, 2006; Boyett et al., 2007; Bruno and Selig, 2007; Haapkylä et al., 2010; Onton et al., 2011) and the Caribbean (Bruckner et al., 1997). This may reflect impaired disease resistance in the host corals under summer conditions, resulting in a shift from natural bacterial communities in the holobiont towards opportunistic pathogens.

While this study fills a gap in the knowledge on coral diseases at Sodwana Bay, further investigations are needed on the drivers and vectors (e.g. corallivorous organisms) of the diseases to improve our understanding of their dynamics and our ability to mitigate their impacts at local and regional scales.

Table 5
Number of fish species and families recorded ≤ 25 m on WIO coral reefs, ranked according to the number of species recorded. Angling records have not been included.

Country	Region/reef	Family	Species	Reference
Tanzania	Mafia Island	56	394	Garpe and Öhman (2007)
Tanzania	Mnazi Bay	47	369	Obura et al. (2006)
South Africa	Maputaland	66	354	Chater et al. (1993)
Madagascar	Andavadoaka	58	334	Gillibrand et al. (2007)
France	Glorieuses Islands	57	332	Durville et al. (2003)
France	Basass da India	49	305	van der Elst and Chater (2001)[a]
France	Juan De Nova	55	299	Chabanet and Durville (2005)
South Africa	Maputaland	50	284	Current study
Tanzania	Pemba Island		244	Richmond and Mohammed (2001)
Mozambique	Southern Mozambique	71	239	Pereira (2003)
Comoros	Mayotte	35	225	Chabanet (2002)
Seychelles	Aldabra	45	221	Downing et al. (2004)
France	Réunion	44	217	Letourneur (1996)
Kenya	Kiunga Bay		208	Church and Obura (2006)
Madagascar	Tulear	44	200	Harmelin-Vivien (1977)[a]

[a] Sampling techniques included underwater visual census as well as other techniques such as rotenone poisoning and/or explosives.

9. Fish community studies

While all of the South African coral reefs lie in a marine protected area, certain reefs are nevertheless open to recreational fishing and SCUBA diving, and the effect of these activities on the fish communities was investigated. This involved a detailed quantitative assessment of the reef-associated fish communities (Floros et al., 2012), yielding an overall diversity of 284 species belonging to 50 families, a species count comparable to other reefs in the Western Indian Ocean (Table 5). Six families contributed > 50% towards the species composition: Labridae, Acanthuridae, Chaetodontidae, Lutjanidae, Pomacentridae and Serranidae. From the results, 26 fish species from ten trophic guilds were selected to develop a fish index in which their presence, absence, densities and size frequencies were used to detect differences in fish community structure on reefs subjected to varying levels of resource use (Floros et al., 2013).

Underwater visual censuses were used to collect the fish data and the results revealed significant differences in fish biomass, abundance and diversity on reefs according to their level of protection (Floros et al., 2013; Fig. 11). The fish abundance and biomass of the selected indicator species were significantly higher in sanctuaries and lower on open reefs. Targeted index species were also larger and more abundant on sanctuary reefs.

Predators were particularly affected by human activity. Firstly, predator abundance and biomass in the multiple-use zones was significantly affected by SCUBA diving, which is a novel finding given the paucity of studies that have documented the effects of this activity on fish communities. All predator categories were well represented on sanctuary reefs, while non-sanctuary reefs were characterized by a higher abundance of prey species. South Africa's coral reefs are among the most heavily dived reefs in the world (Schleyer and Tomalin, 2000 cf. Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Hawkins et al., 2005) and the decline in top predators on certain reefs was linked to this intensive diving pressure (Floros et al., 2013). Secondly, predator biomass in the no-take sanctuary zones constituted 80% of the total fish biomass, which was threefold higher than that in the multiple-use zones. On a global scale, this is comparable to the fish biomass recorded on undisturbed coral reefs in the North Western Hawaiian Islands and Northern Line Islands (Floros,
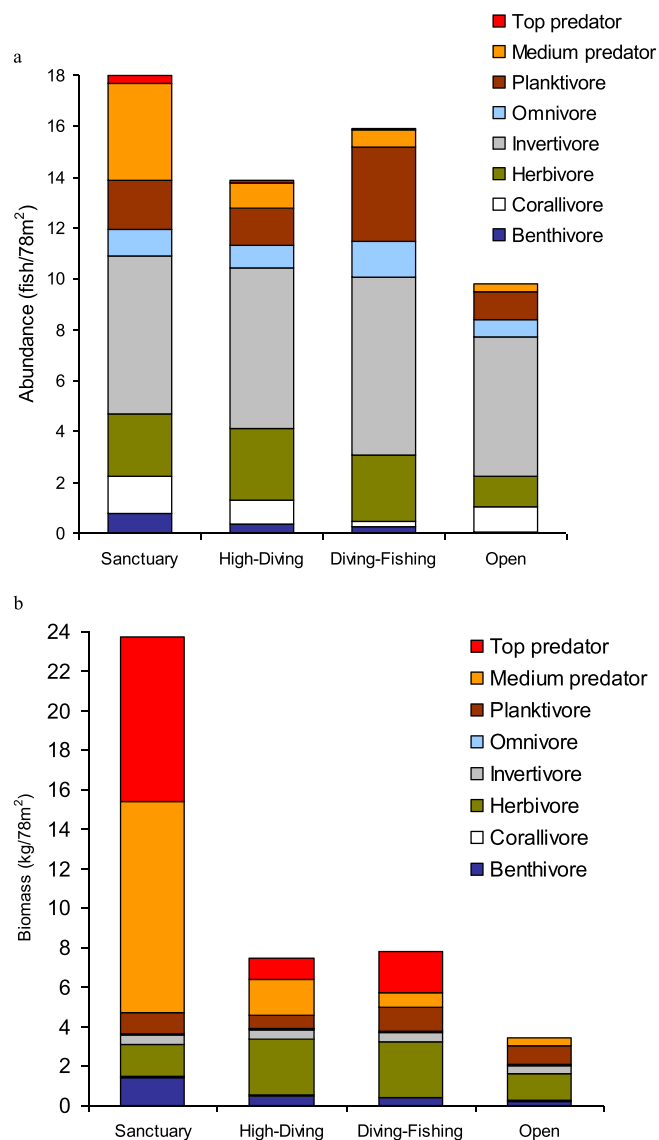

Fig. 11. Total abundance (a), biomass (b) and trophic structure of selected fish species on multiple-use and no-take sanctuary reefs in Maputaland.

2010). Such high predator biomass values on coral reefs are rare due to overfishing of predators on a global scale (DeMartini et al., 2008) and it has been proposed that the no-take sanctuaries should be viewed as benchmark ecosystems.

The data thus revealed that recreational fishing and high diving intensity are influencing the fish community structure on southern African coral reefs. This was confirmed by general linear model (GLM) analysis which indicated that human activities are more responsible for the variance in the fish assemblages than environmental variables such as depth, topography and coral cover (Floros et al., 2013). Long-term monitoring of these fish communities was recommended to confirm the trends observed in the data. The results also indicated that sanctuary reefs are fulfilling their role in conserving the biological integrity of the fish communities, highlighting the importance of such no-take zones.

A distinctive feature of South Africa's coral reefs is that they are not located in close proximity to mangrove or seagrass systems. This is unusual because mangroves and sea grass beds are used by numerous coral reef organisms during different stages of their life cycles and different diurnal or seasonal cycles (Laegdsgaard and Johnson, 2001; Nakamura and Sano, 2004; Scheibling and Metaxas, 2009). The ontogenetic migration of fish from mangroves and seagrass beds to coral
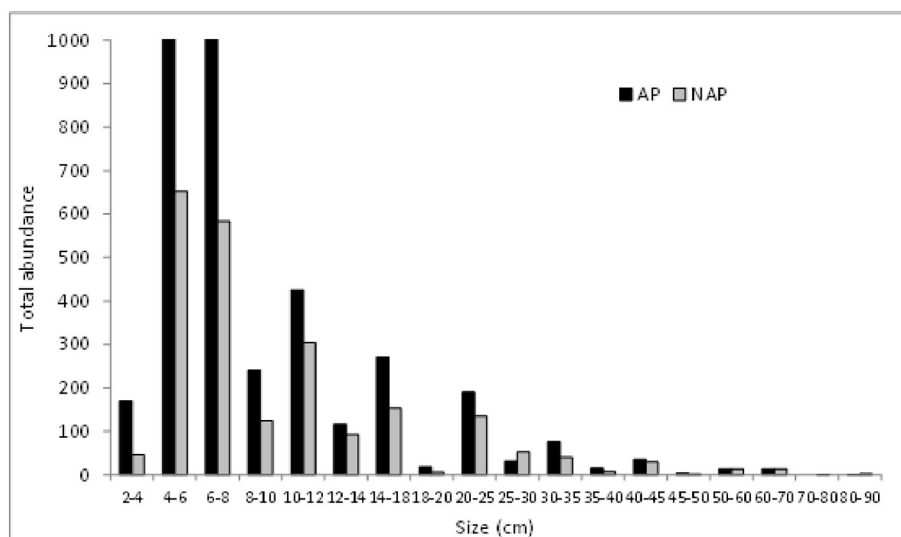
Fig. 12. Size distribution of fish species recorded within *Acropora austera* (AP) and non-*A. austera* (NAP) habitats at Sodwana Bay.

reefs is of importance (Dorenbosch et al., 2005; Mumby et al., 2004; Mumby, 2006; Nagelkerken et al., 2002) and the absence of these ecosystems from the proximity of the South African coral reefs suggests that specific micro-habitats within the coral reef must provide habitat for juvenile fish (DeMartini and Anderson, 2007; Garpe and Öhman, 2007).

Acropora austera is the only branching species on South Africa's reefs that forms large monospecific stands with high structural complexity (C. Floros, pers. obs.). A recent study revealed that reef areas with *A. austera* patches hosted greater fish diversity and higher numbers of juveniles than areas without such patches (Floros and Schleyer, 2016; Fig. 12). The importance of reef structural complexity in shaping fish communities is well known, but the results revealed a high dependency by a number of fish species on a single coral species at Sodwana Bay, at a critical stage in their life-history. Several large patches of *A. austera* have been diminishing on the Sodwana reefs over the last decade and there is little evidence of their replacement or regrowth. Branching acroporids are among the species that are highly susceptible to stressors that currently threaten coral reefs, such as physical damage (McManus et al., 1997; Lamb et al., 2014), climate change (Loya et al., 2001; Obura, 2001) and disease (Alvarez-Filip et al., 2009; Ruiz-Moreno et al., 2012). Thus the loss of *A. austera* due to bleaching or episodic storms, for example, may have a significant ecological impact on the reef fish communities.

Fish stocks are globally depleted and this is also true of South African reef fish communities. An understanding of the connectivity of reef fish stocks is thus imperative for their management since, once depleted, the question arises as to whether replenishment will occur from adjacent reefs. This is particularly important on South African coral reefs as they are separated and isolated by extensive stretches of sandy substrata. Connectivity studies have thus been initiated on two representative fish most affected by the aforementioned anthropogenic activities, *Epinephelus tukula* by SCUBA diving and *Aprion virescens* by fishing (Floros, unpub. data). These embrace acoustic monitoring of the movement of acoustically tagged adults and gene flow between the populations.

In conclusion, the South African coral reef communities have high fish diversity despite being the southernmost coral reefs in East Africa. Indo-Pacific species predominate, suggesting that they may be linked to northern coral reefs in the Western Indian Ocean. While MPAs have protected the reef fish communities from numerous threats that have reduced fish populations on many tropical reefs, human activities are still having a negative effect in the multiple-use zones. Fortuitously, no-

take sanctuary zones represent undisturbed reefs that may constitute benchmark communities for other high-latitude coral reefs. The decline in *A. austera* abundance is concerning and highlights the vulnerability of fishes to the loss of coral and reef structural complexity.

10. Economic valuation of the reefs at Sodwana Bay

Coral reefs have been shown to provide economic value to communities that reside in the adjacent coastal zones (Wielgus et al., 2003). They are characterized by high biodiversity (Berg et al., 1998) that provides food and income as cardinal measurable benefits (Berg et al., 1998; Brander et al., 2007; Burke et al., 2008; Cesar et al., 2003; Cesar and van Beukering, 2004; Conservation International, 2008; van Beukering et al., 2007). Indirect benefits that they provide include habitat, refuge and nursery functions (Brander et al., 2007; Moberg and Folke, 1999), ecological resilience (Rudd et al., 2001) and shoreline protection (Cesar and Van Beukering, 2004), including sediment generation and entrapment.

A primary purpose for the promulgation of marine protected areas is the conservation of fragile ecosystems (Davis and Tisdell, 1995). This has tourism benefits as users assume that protected reefs are healthier and have greater biodiversity than their unprotected counterparts (Hawkins et al., 2005). It has been noted that the reefs in the iSimangaliso Wetland Park are subjected to varying levels of protection, some being open to SCUBA diving and recreational fishing. Before the turn of the century, Schleyer and Tomalin (2000) had noted that these human activities had negative effects on the coral communities. Further growing threats such as climate change and coral bleaching indicated that an economic valuation of the reefs was warranted to establish the long-term effects of such change on their human benefit.

Sodwana Bay is central along the coast of the iSimangaliso Wetland Park (Fig. 1) and is the area most used by the public, driving a local economy reliant upon reef-based tourism. A 2005 study by Mograbi and Rogerson (2007) revealed that the tourism associated with SCUBA diving created 404 permanent and 233 casual jobs at Sodwana Bay. Employment in the uMhlabuyalingana Municipality, in which Sodwana Bay is located, is low (13%), illustrating the importance of this job creation (Mograbi and Rogerson, 2007).

Coral reefs attract SCUBA divers, at least in part due to the good visibility, warmth and biodiversity that is associated with them (Hawkins et al., 2005; Moberg and Folke, 1999; Parsons and Thur, 2008; Schleyer and Tomalin, 2000). In 2009, the coral reefs at Sodwana Bay were rated 15th out of 100 sites reviewed in a UK SCUBA magazine

Table 6
Economic value of the coral reefs at Sodwana Bay.

Economic generator	Annual value – ZA Rand	Annual value – USD
SCUBA diving	57 101,000–65 883,000	4,267,728–4,924,095
Boat-based angling	11,604,000–19,760,000	867,283–1,476,862
Sediment generation	2,567,000–4,797,000	136,562–253,614
Sediment entrapment	71,819,000–84,567,000	5,367,752–6,327,264
Total	143,091,000–175,097,000	10,639,325–12,981,835

(Scuba Travel, 2009) for such qualities. A recent study revealed that these reefs attract divers from each of South Africa's nine provinces as well as 21 foreign countries (Laing et al., 2018a). At least 13,000 trips are conducted annually by divers to Sodwana Bay, ~12,000 by South Africans, and 98% of the latter indicated that diving was the primary purpose for their visit. Most of this activity is focused on Two-mile Reef, the closest to the launch site at Jesser Point (80%–88% of ~65,000 dives per year). In terms of value, their travel costs constituted ZAR10M as consumer surplus per year. When totalled with the amount that they spend on their trips – their accommodation, diving, refreshment and curio purchases – the industry involves ZAR57 101,000 – ZAR65 883,000 direct expenditure per year (see Table 6; Laing et al., 2018b). This figure excludes the associated underlying results of such expenditure, such as jobs created and families supported by the tourism.

Game fishing is a popular pastime of marine boat-based anglers in South Africa. The north-east coast of South Africa is the primary destination for this activity, with Sodwana Bay being among the most popular (Crous, 2000). Annually, ~17 game fishing competitions are held at Sodwnana Bay (Kyle, Ezemvelo KwaZulu-Natal Wildlife, 2012, pers. com.; Kyle, 2016). Pelagic fish are targeted as bottom fishing is prohibited in the iSimangaliso Wetland Park, comprising mainly fish in whose life cycle reefs play an important role. A high investment in fishing assets characterises the anglers involved but their capital expenditure cannot be completely attributed to fishing at Sodwana Bay; however, evaluation of their reliance on coral reef-associated species enabled discount of these values to the relevant Sodwana Bay costs (Laing et al., 2018a). This was estimated to be between ZAR11M – ZAR19M p.a. (Table 6). This value is nevertheless considered an underestimate of the revenue that anglers bring to Sodwana Bay annually.

The coastline within the iSimangaliso Wetland Park has been described as sediment-starved (Green and Uken, 2008); limited inflows of sand and sediment and the high transport velocity of the Agulhas Current are the cause of this (Green and Uken, 2008; Ramsay, 1996; Shaw, 1998). Considerable sediment movement occurs in the inshore zone due to the powerful north-trending wave pattern which moves up to one million m^3 of sediment past any fixed point annually (Ramsay, 1996; Shaw, 1998; Smith et al., 2010).

Coral reefs in the iSimangaliso Wetland Park generate bioclastic sediment and create a barrier between the shoreline and the narrow continental shelf, resulting in sediment entrapment and accumulation in the inshore zone (Green, 2009; Martin and Flemming, 1986; Ramsay, 1996; Shaw, 1998). They consequently assist in sediment retention, sediment that would otherwise be lost to deeper offshore zones. The coastal lake systems of Maputaland appear to be protected by this 'reef process' and the Kosi, Sibaya and St Lucia systems are not as 'open' as Richards Bay to the south, which lacks such reef protection.

Submarine canyons adjacent to some of the reefs accelerate the loss of sediment as sand moving past the reefs is funnelled into them (Ramsay, 1996). The volume of sediment that would probably be lost from Sodwana Bay in the absence of its reefs was estimated to be 880 300m^3–1056 300m^3, comprising 30,321 m^3–56,311 m^3 no longer generated by the reefs and 850,000 m^3–1,000,000 m^3 lost through slumping into the deep offshore zones (Laing et al. submitted).

The Maputaland reefs thus provide ecosystem services in the form of sediment generation, sediment retention and shoreline protection.

The value of this sediment generation and entrapment was assessed

for the Sodwana coral reefs using the replacement cost (RC) method (Chee, 2004; Farber et al., 2002). Sediment replacement by dredging was identified as being the least costly option, this being one of the criteria of the RC method (Freeman et al., 2003), as well as one that has been established internationally (Kim, 2007). However, it must be realised that sediment replacement by dredging would not provide identical ecological services in e.g. food provision for microorganisms, habitat replacement or wave energy dissipation, neither would it fulfil the same aesthetic and recreational use functions.

The cost, in this case the hypothetical cost of dredging, would have to be willingly borne by the public to satisfy the RC method (Freeman et al., 2003). Such willingness was confirmed in a survey that was carried out with beach users at Sodwana Bay who were questioned regarding their willingness to pay for such a solution, totalling ZAR74M – ZAR89M per year (Table 6; Laing et al., 2018b).

In US dollar terms, the sum of these values equates to $10639325–12,981,835 per annum at the exchange rate at the time of writing (ZAR13.45 per US dollar). In terms of reef area, the above values equate to $33,118.5 - $40,410.4 per hectare, as the central reef complex is 321.25 Ha in size. This provides an estimate of the rehabilitation costs that could be considered viable in the event that the reefs were damaged. These values, however, are underestimates, as they do not include the employment associated with the reefs (the secondary economy that relies on the tourism they attract) or ecosystem service values that are difficult to quantify in the absence of markets. These are likely to be greater than the monetary values presented here in terms of a loss in ecological function that would affect the quality of the coral reefs, resulting in a negative impact on Sodwana tourism.

11. Final considerations

The research reviewed here has yielded much valuable information. It has firstly provided baseline information on relatively pristine, high-latitude reefs that are, by and large, well-protected. They have nevertheless manifested minor bleaching associated with ENSO events at a bleaching threshold in the region of 28.5 °C. This is lower than the bleaching threshold at lower latitudes, which is to be expected as the local corals are acclimated to high-latitude conditions.

While temperatures have (temporarily?) plateaued since the turn of the 21st century, slow but consistent changes in the coral community structure have emerged during long-term monitoring. These may be accompanied by changes in the distribution of corals and two examples of this were presented earlier. More important, however, will be subtle changes in coral resilience when the corals are stressed as they approach the bleaching threshold and Séré et al. (2015a) reported an increased incidence and susceptibility of corals to disease with a rise in temperature.

The marginal nature of the South African coral reefs in terms of temperature, light and aragonite saturation (Kleypas et al., 1999) will render them sensitive to global change. Light will remain constant but temperature could become more important. Limited determinations of aragonite saturation (Ω-arag) at Sodwana Bay have yielded a mean value of 3.6 over much of the year (unpub. data); only in winter have values been lower ($\Omega x = 2.9$). Kleypas et al. (1999) considered the cut-off value of aragonite saturation for reef accretion to be 3.4 and, on this basis, included the South African coral reefs in the 'non-reef' category. Yet aragonite saturation values higher than this on the Maputaland reefs, possibly attributable to frequent, turbulence-driven remobilisation of the sediments, again point to temperature as being more important. Ocean acidification may thus not have a remarkable effect on the reefs.

The coral reefs in Maputaland (and similar high-latitude reefs) may prove to be 'canaries in the coalmine' regarding the future of corals in respects different from reefs at lower latitudes. Being deeper (minimum depth 8 m), they will be less affected by warm surface water advected onto the shelf by the Agulhas Current and may become refugia. On the

other hand, some authors expect the Agulhas Current to strengthen and warm with climate change (Roualt et al., 2009), increasing the likelihood of warm water intrusion. However, more recently, it has been shown that the Agulhas Current is merely getting broader as a result of greater eddy activity (Beal and Elipot, 2016); the jury thus remains out on the long-term effects climate change may have on the oceanography in the region. If warm current advections do increase, they may nevertheless be moderated by cooler upwelling associated with cyclonic eddies.

The effects of global warming could have wider implications on the Maputaland reefs. Changes in coral community structure caused by coral bleaching could be deleterious to fish populations as coral species that contribute to reef complexity and are more susceptible to bleaching die, reducing the nursery potential of the reefs. Gross mortality of the corals would have even more severe implications and the effects would include reduction of the sediment budget in the region with the loss in bioclastic sediment generation. Erosion of the underlying Pleistocene sandstone may occur without the protective coral veneer and a gradual reduction of the reefs may eventually diminish their value in shoreline protection. The situation is exacerbated by discontinuity in the reef systems; their low connectivity and the high levels of self-seeding demonstrated among the corals indicate that the reefs are individually vulnerable, and may not readily recover from severe mortality. This is borne out by observations of areas affected by crown-of-thorns starfish predation in the past (Celliers and Schleyer, 2006) and dead *A. austera* patches currently under investigation.

Mather et al. (2009) and Mather and Stretch (2012) considered other anticipated consequences of global warming on the East Coast of South Africa, viz. sea-level rise and an increase in episodic storms. While sea level is presently rising at just under 300 mm per century, Mather and Stretch (2012) undertook projections of the effects of increases in sea level of 300 mm, 600 mm and up to one metre to 2100. Since the Maputaland reefs are relatively deep, such changes will probably have minimal effects on the coral communities; they are already adapted to living at depth. Storm surges, however, are expected to increase globally (Webster et al., 2005), and will result in increased damage to the corals (particularly the aforementioned *A. austera* patches) as well as greater mobilisation of the sediments. While the latter may be deleterious to the coral communities, it will also affect the sediment budget in the region and the rate of erosion of the shoreline.

The reefs have considerable use and service value which any degradation in their condition would diminish. This would affect tourism to the iSimangaliso Wetland Park and negatively affect the already impoverished local economy. The fact that most marine tourism in the Park is centralised at Sodwana Bay, the core region of its coastal environment, is anomalous; its marine sanctuaries lie in what should be buffer zones at its periphery in the northern and southern reef complexes (Fig. 1). This anomalous situation dictates that careful management and monitoring of the central reef complex is paramount and consideration should be given to proclaiming the northernmost of the reefs in this complex (Nine-mile Reef) as a sanctuary. This is the least visited reef as it is the furthest from the launch site; it has high genetic diversity and is close enough to the other reefs in the complex to provide larval replenishment via the prevailing current flow; and it would provide a benchmark for monitoring condition on the reefs subjected to relatively high use.

Notwithstanding the foregoing, the South African coral reefs are in good condition and provide room for optimism regarding the future of corals at high latitude. They furthermore provide a natural laboratory for the study of these systems under protected and relatively pristine conditions, and are currently under further investigation regarding their responses to climate change in terms of accretion versus bio-erosion and coral gene expression.

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